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Succession, diversity and feeding habits of microarthropods in decomposing birch leaves

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With 6 figures

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1. Introduction

Decomposition is a fundamental process in all ecosystems. It is desirable to understand both the role of decomposition in relation to the function of the whole ecosystem, and also how decomposition processes are performed and regulated. Both questions require "case studies" as a base.

The present work is part of a "case study" on the decomposition of birch leaves. While dry weight loss and chemical changes of the leaves have been published earlier (HÅGVAR & KJØNDAL 1981), this paper concerns the changes in the microarthropod fauna (Acari and Collembola) during decomposition. These groups are very abundant in forest soil and participate in all stages of decomposition. Because of their high numbers and richness in species, they are suitable for the study of zoological succession during various decomposition phases. Such information is necessary to understand the function of soil animals in the recycling of plant nutrients.

There are few studies in which the development of the soil fauna has been followed over a long time in forest litter. In studies covering only one year, it is difficult to distinguish successional changes from natural seasonal variations. Long-term studies indicating successional changes in the microarthropod fauna of forest litter are those of METZ & FARRIER (1969) and ANDERSON (1975).

As in the work of ANDERSON (1975), the development of faunal diversity and the gut contents of dominant species have been investigated. In addition, horizontal variations in the succession pattern were studied, and the leaf litter fauna was compared with that of the surrounding soil.

Most of the material on Oribatei succession was presented as part of a thesis at the University of Oslo (KJØNDAL 1980). The rest of the Microarthropod material, gut contents analysis and writing were the responsibility of the first author.

This investigation is part of a larger research programme studying effects of acid precipitation on forests and on fish (the Norwegian SNSF-project). During recent decades, the acidity of rain and snow has increased markedly over large parts of Europe and North America, due to long-range transported industrial air pollutants (DOVLAND et al. 1976; OECD 1977, LIKENS et al. 1979). The effects of artificial acid rain on decomposition rate and birch leaf chemistry were included in the paper by HÅGVAR & KJØNDAL (1981), while the effects of artificial acidification on microarthropod succession in birch leaves will be described later.

2. Material and methods

The study site was a clear-cut area in a forest consisting mainly of Norway spruce (*Picea abies* (L.) KARST.) and Scots pine (*Pinus sylvestris* L.), about 40 km north of Oslo. *Deschampsia flexuosa* (L.) TRIN. dominated the vegetation, which belonged to the Eu-Piceetum Myrtilletosum type. The forest was situated on a flat plain of glaci-fluvial sandy deposits and had developed a podzol profile (Typic Udipsamment, USDA classification) with a 3 cm thick organic layer (O) and a bleached horizon (Ae) of a corresponding thickness. Detailed information on the site can be found in ABRAHAMSEN et al. (1976) and STUANES & SVEISTRUP (1979).

Small experimental plots (4 × 4 m) were used, containing 36 small birches (*Betula verrucosa* EHRH.) planted in 1974, a half year after the clear-cutting. In 1978, at the end of a three year long experimental period, the birches measured 1.1 m on average. While birches are rare in mature forest at this site, they often occur naturally in the first phase after clear-cutting.

To be able to identify the leaves under study, and to take samples without losing the most active animals, the litter bag technique was used (CROSSLEY & HÖGLUND 1962). Although natural leaf litter is packed horizontally on the ground, such an arrangement in the bags would not allow the animals to escape from the sample during extraction. A cylindrical litter bag type was therefore constructed, 3 cm high and with a diam. of 6.5 cm, in which the leaves were packed vertically. The bags were made of nylon net with 1 mm mesh size. Each was filled with 6.85 g (dry weight) of leaves, which had been collected during leaf fall the previous year. The leaves were a mixture of two species (*B. verrucosa* and *B. pubescens* EHRH. in a ratio of approximately 1:2).

On 28 July 1975, the bags were placed into the O-layer, so that the upper surface was at the same level as the litter surface. This was found necessary to avoid drying out during the warm summer months. There were four samplings, in which the following mean dry weights were noted on untreated plots: Sampling I (19. 9. 1975): 6.15 g, sampling II (28. 4. 1976): 5.29 g, sampling III (2.—9. 11. 1976): 5.12 g, and sampling IV (10. 11. 1978): 4.30 g. The first sampling was made only one month before a permanent snow cover was formed, and the second just when the last snow melted away. Chemical changes of the leaves during decomposition have been described by HÅGVAR & KJØNDAL (1981).

A total of 306 litter bags were used for analysis of animal succession (numbers from each sampling were 32, 68, 128 and 78, respectively). Originally, it was intended to describe succession by using only bags from unwatered plots, i.e. four plots, as the whole experiment including acidification had been designed with four replications. However, material from untreated plots showed no significant differences from material collected at plots given ground water (pH 6) or water acidified to pH 4 or pH 3. Bags from these treatments were therefore pooled to give better estimates of microarthropod populations. An exception was made for Brachychthoniidae and *Tectocephus velatus* (MICH.) [Oribatei] at the pH 3-treatment, sampling IV, due to rather high values.

Because of the very time-consuming work of counting and identifying certain mites, especially the smallest ones, limitations were set for the counting of several groups. Thus, for Mesostigmata, Astigmata, Prostigmata, Brachychthoniidae and juvenile Oribatei, the description of succession was based upon not-watered and pH 6-watered plots at sampling I (16 bags), not-watered plots at sam-

plings II and III (16 of the bags each time), and at sampling IV 16 of the bags from pH 6-treated plots for Mesostigmata, and 54 bags from not-watered, pH 6- and pH 3-treated plots for the rest of the mites in question.

In all figures, the indicated SE has been calculated from the mean values of the four replications, not from individual bags or plots.

The monthly precipitation and mean temperature during the experimental period has been given by HÅGVAR & KJØNDAL (1981).

A parallel experiment was run for a three-month period in a greenhouse (November 1977 to Februar 1978), using a smaller, cylindrical litter bag type inserted into forest soil of a similar kind, which was kept in drained plastic containers (for details see HÅGVAR & KJØNDAL 1981). There were two categories of leaves: "freshly" fallen leaves as in the field experiment, which lost 37% dry weight during the period (corresponding to three years' weight loss in the field), and "old" leaves having already lost 40% dry weight and reduced by an additional 16% during the experiment. The microarthropod fauna of these two leaf categories was also studied and may help to illuminate the faunal change in a more advanced stage of decay than achieved in the field experiment.

Extraction of microarthropods from litter bags was performed according to MACFADYEN (1961).

3. Results

3.1. Faunal changes during decomposition

3.1.1. *Collembola* species

The abundance and dominance of the most common *Collembola* species encountered in field litter bags is illustrated in Figure 1. Already at the first sampling, a rich *Collembola* fauna had been established, regarding both abundance and species numbers. However, two species made up $\frac{3}{4}$ of the material: *Entomobrya corticalis* and *Lepidocyrtus cyaneus*. These species seem to have the character of "pioneer species", as both were much less numerous in all later samplings. Three other species also showed greatest abundance at the first sampling: *Lepidocyrtus lignorum*, *Hypogastrura inermis* and *Entomobrya nivalis*.

A very marked change in the *Collembola* fauna occurred between first and second sampling, i.e. during late autumn and winter. At snow melt, all pioneer species were scarce, but another species, *Friesea mirabilis*, had effectively colonised the bags and represented more than half of all *Collembola*. At the two later samplings, the population of the species was low again.

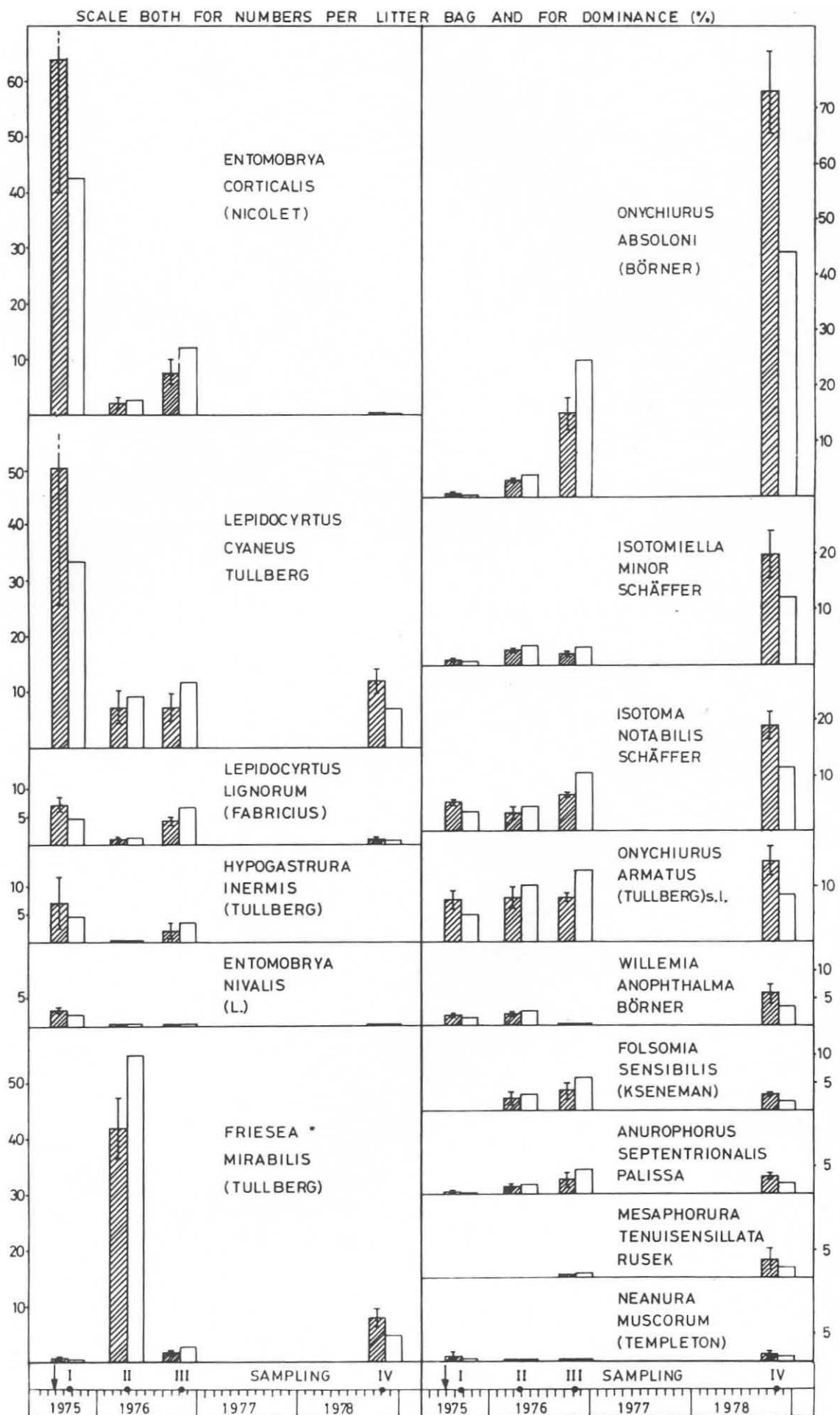
One species, *Onychiurus absoloni*, was characterized by a steady and steep increase in abundance as decomposition proceeded. The abundance at the last sampling was higher than that achieved by any of the species characteristic of the early phases, and almost every second *Collembola* in the bags belonged to this species.

Two other species became more abundant at the last sampling: *Isotomiella minor* and *Isotoma notabilis*, together representing $\frac{1}{4}$ of all *Collembola*. The next common species was *Onychiurus armatus* s.l., also somewhat increasing its mean abundance compared to earlier samplings. Four less common species were found most numerous in the third or fourth samplings: *Willemia anophthalma*, *Folsomia sensibilis*, *Anurophorus septentrionalis*, and *Mesaphorura tenuisensillata*. *Neanura muscorum* was found in very low numbers in all samplings.

The other *Collembola* species recorded (< 1 per bag) will be presented later in Table 1.

3.1.2. *Oribatei* species

In parallel with *Collembola*, there were *Oribatei* species which must be considered as "pioneer species", although their abundance was reduced more gradually (Fig. 2). The most prominent among them were *Oribatula tibialis* and *Autogneta trågårdhi*, together representing more than half of all *Oribatei*, and $\frac{3}{4}$ of the adult *Oribatei*, at the first sampling. Their abundance was similar to that of the two *Collembola* "pioneers", *Entomobrya corticalis* and *Lepidocyrtus cyaneus* (Fig. 1). Both *Oribatei* species were also abundant at the second sampling, but became gradually scarce through the third and fourth samplings. *Eupelops duplex* was the third common species at the first sampling, the second most abundant at the next sampling, and the dominant *Oribatei* at the third sampling. However, like the two other species, the abundance dropped markedly at the last sampling.



Two other species, with a low abundance, seemed to be represented mainly in the early stages of decomposition: *Adoristes poppei* and *Chamobates incisus*.

The right half of Fig. 2 illustrates groups or species which were most numerous in the later phase. Brachychthoniidae and adult Phthiracaridae were the two most abundant groups among Oribatei at the last sampling. Among Phthiracaridae, the genus *Steganacarus* dominated, followed by *Phthiracarus* sp. Also *Porobelba spinosa* and the genus *Suctobelba* sp. were well represented in the Oribatei material, while three of the depicted species were less numerous: *Brachychochthonius zelawaiensis*, *Carabodes forsslundi* and *Paulonothrus longisetosus*.

In Fig. 3, the left half shows abundance and dominance data for ten species of Oribatei, which belonged to neither the "pioneer" nor the "late" category. Species which never reached an abundance above one animal per bag, are listed in Table 1.

3.1.3. Mesostigmata species

Contrary to Collembola and Oribatei, there were no species of Mesostigmata which showed drastic variations in abundance during the field experiment. No species ever reached an abundance above ten animals per litter bag (Fig. 3). However, some trends shall be pointed out. *Hypoaspis forcipata* was the most abundant species at the two first samplings, but then disappeared at the third and was very scarce at the fourth sampling. Five species had their highest mean abundance at the last sampling: *Veigaia nemorensis*, *Pergamasus* cf. *lapponicus*, *Prozercon kochi*, *Parazercon sarekensis*, and *Eviphis ostrinus*. *Pergamasus parrunciger* was well represented at both the third and fourth samplings, and made up almost half of the total Mesostigmata numbers at the third sampling.

3.1.4. Astigmata species

Within Astigmata, large changes in abundance and dominance occurred between different species during the experiment. At the first sampling, Astigmata alone amounted to more than three hundred animals per bag, surpassing the total abundance of Oribatei and representing almost 40% of all Acari (Fig. 4). More than 99% of the Astigmata were accounted for by *Tyrophagus* cf. *fungivorus*. The abundance was much lower on the second and third samplings. At the last sampling, the species was completely absent from the bags.

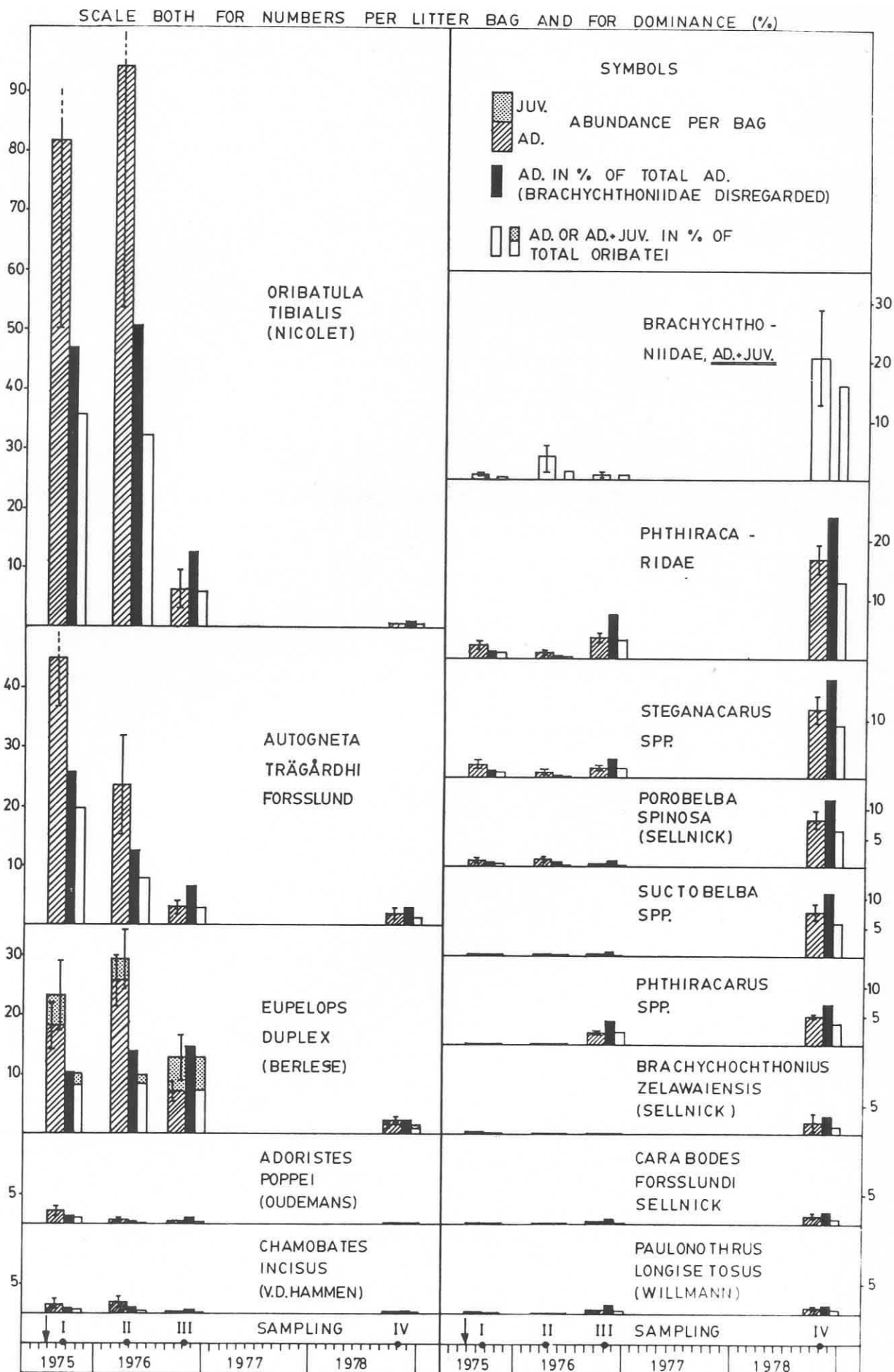
Another species, *Schwiebea* cf. *nova*, behaved opposite to this. The abundance was about two animals per bag at the first sampling, then about ten at the two next samplings, and well above one hundred at the end of the experiment, at which time they represented 97% of total Astigmata and were comparable in numbers to Oribatei (Fig. 4).

3.1.5. Abundance at group level

In Collembola, Astigmata and Prostigmata, there was a common pattern in population changes from sampling to sampling (Fig. 4). From a high abundance in the beginning, the abundance dropped gradually through the two next samplings, but increased again markedly at the last sampling. Oribatei showed a similar pattern, but with high abundance in both two first samplings and with a less marked increase in the fourth, after the drop. Mesostigmata, however, did not follow this trend. The total abundance was practically unchanged during the three first samplings, and then increased somewhat.

Total Microarthropoda followed the same main pattern as Collembola, Astigmata and Prostigmata (Fig. 4). The highest abundance was at the first sampling, while the lowest abundance noted, one year later, was one fourth of that. If we correct for weight reductions of the litter during decomposition, the mean abundance of Microarthropoda per g litter was slightly higher at the last than at the first sampling (Fig. 4, bottom right).

Fig. 1. Changes in abundance per litter bag (hatched columns) and in dominance (% of total Collembola, open columns) for the most numerous Collembola species in decomposing birch leaves. Left: species with highest abundance in the early phase. Right: species with highest abundance in later phases. Vertical lines indicate standard error of the mean (SE). Starting point (arrow) and sampling times are shown at the bottom.



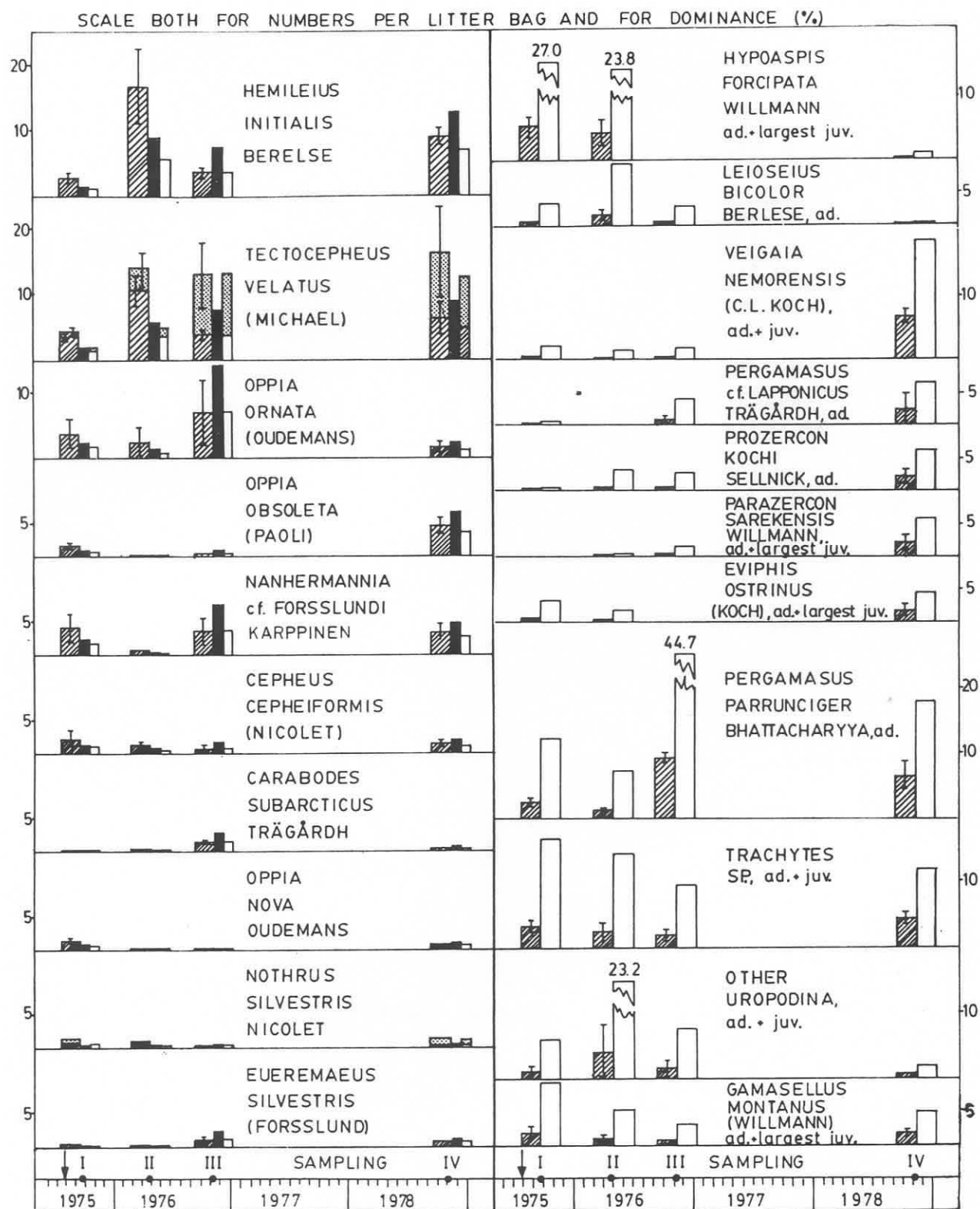
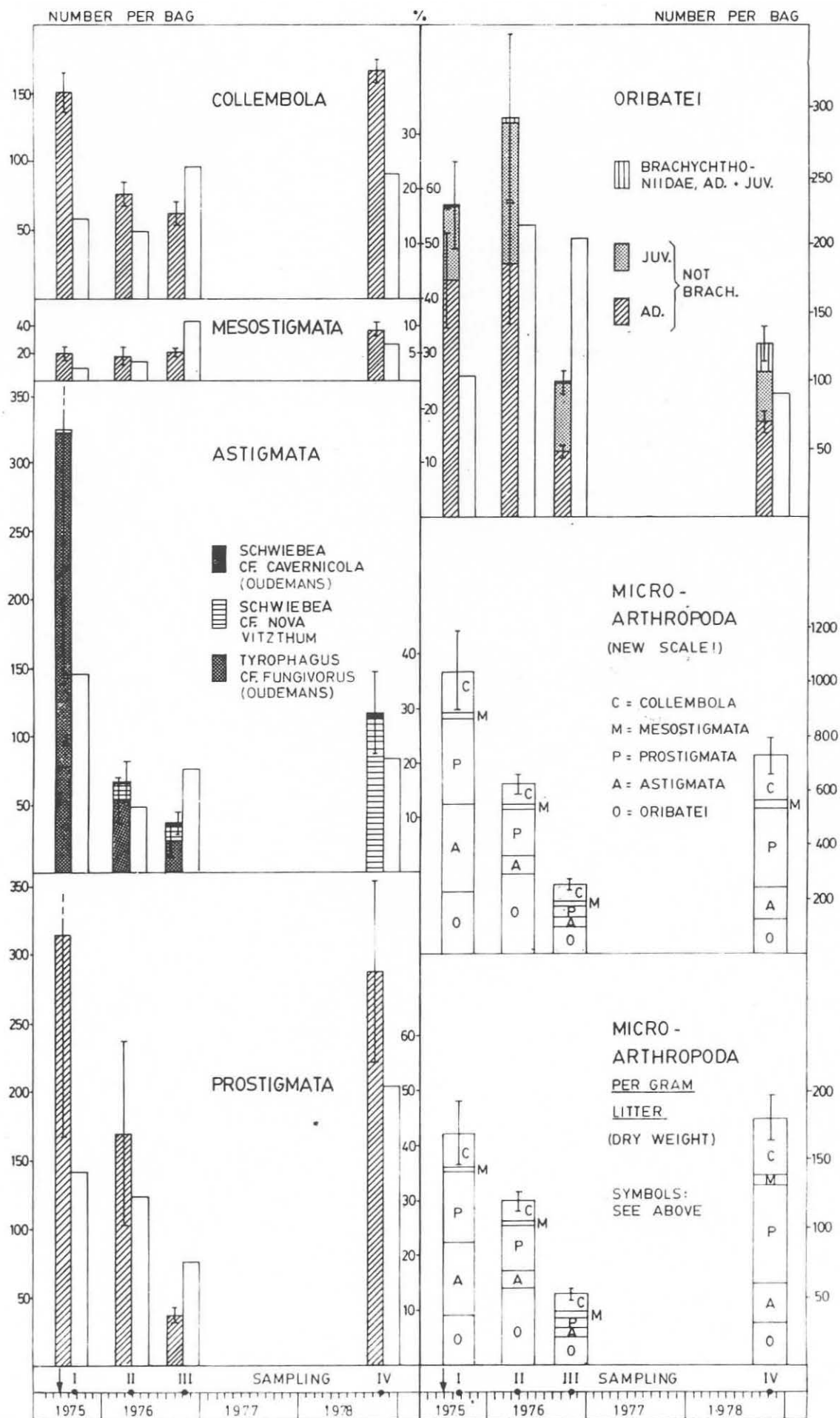


Fig. 3. Changes in abundance per litter bag and in dominance for certain Oribatei species (left and for the most abundant Mesostigmata species (right) in decomposing birch leaves. Symbols for Oribatei are explained in Fig. 2, and for Mesostigmata in Fig. 1. Vertical lines indicate standard error of the mean (SE). Starting point (arrow) and sampling times are shown at the bottom.

Fig. 2. Changes in abundance per litter bag and in dominance for certain Oribatei species in decomposing birch leaves. Symbols are explained at top right. Left: species with highest abundance in the early phase. Right: species with highest abundance in later phases. Vertical lines indicate standard error of the mean (SE). Starting point (arrow) and sampling times are shown at the bottom.



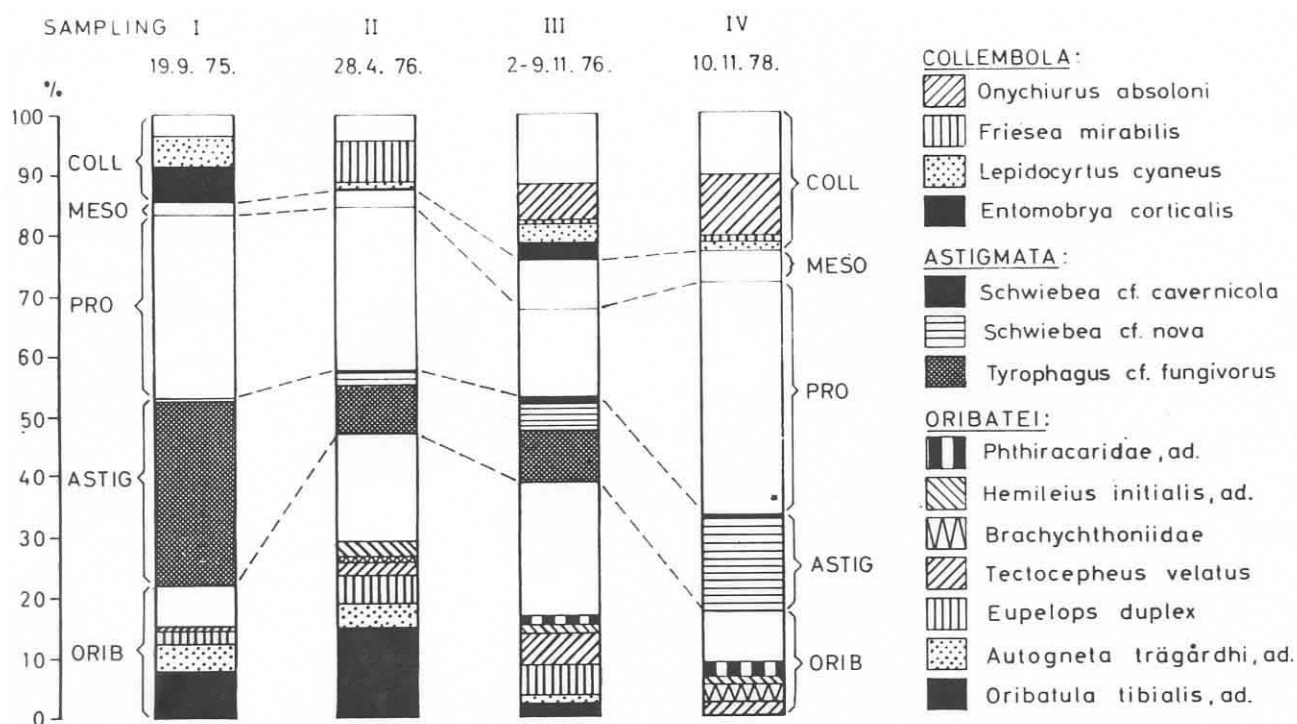


Fig. 5. Changes in dominance within the microarthropod community in decomposing birch leaves (litter bags laid out 28. 7. 1975).

3.1.6. Dominance

The percentage composition of the microarthropod community at the various samplings, with main groups and the most common species or families indicated, is depicted in Fig. 5. Oribatei, Astigmata and Prostigmata could each, at various times, make up considerable proportions of the total. Collembola achieved a maximum of 24%, and Mesostigmata only 8%.

Marked changes in the overall picture occurred from sampling to sampling. A very large proportion at the first sampling consisted of "pioneer" species which later became insignificant (*Lepidocyrtus cyaneus*, *Entomobrya corticalis*, *Tyrophagus cf. fungivorus*, *Autogneta trågårdhi*, *Oribatula tibialis*). The most conspicuous change during the first late autumn and winter was the reduced dominance of *Tyrophagus cf. fungivorus* which gave Oribatei the high dominance of almost 50%. In the same period, *Friesea mirabilis* became the most abundant Collembola. At the third sampling, Prostigmata were relatively scarce, while the dominance of Collembola and Mesostigmata had increased. Oribatei still represented a substantial part of the total, about 40%. On lower systematic levels, changes were evident in both Collembola, Astigmata and Oribatei. The most important Collembola species at this time, *Onychiurus absoloni*, had been found as only a few specimens at the two first samplings. Within Astigmata, we see that *Schwiebea cf. nova* to a large degree has replaced *Tyrophagus cf. fungivorus*. In Oribatei, *Tectocephus velatus* and *Eupelops duplex* were now the most dominant species, and the box mites (Phthiracaridae) had come into the picture.

Fig. 4. Changes in abundance per litter bag and in dominance of major microarthropod groups in decomposing birch leaves. Open columns in Collembola indicate percentage of total Microarthropoda, while open columns in Mesostigmata, Astigmata, Prostigmata and Oribatei indicate percentage of total Acari. The total abundance of microarthropods at various samplings is also shown, both per litter bag and per gram litter (dry weight). Vertical lines indicate standard error of the mean (SE). Starting point (arrow) and sampling times are indicated at the bottom.

From the third to the fourth sampling several of the changes observed from the second to the third sampling were reinforced. Collembola became totally dominated by *Onychiurus absoloni*, practically all Astigmata were *Schwiebea* cf. *nova*, and Phthiracaridae became still better established. In addition, Brachychthoniidae became abundant, slightly surpassing Phthiracaridae. On the group level, Prostigmata again increased their dominance at this last sampling, while Oribatei achieved the lowest dominance value measured during the experiment (below 20 %).

3.1.7. Species numbers and diversity

The occurrence of Collembola, Oribatei and Mesostigmata species with low abundance (never above one per litter bag) is shown in Table 1, together with total number of species and the Shannon-Wiener index of diversity (SHANNON & WIENER 1963). This index is $H' = -\sum_{i=1}^S p_i \ln p_i$, where S is the number of species and p_i is the percentage of each species. The changes from sampling to sampling are further indicated by the number of species new to the system, number of species regained (after temporary loss), number of species lost since last sampling, and number of species permanently lost (within the frame of the investigation). Altogether, 31 Collembola species were recorded, 49 Oribatei species and 15 Mesostigmata species. The real numbers were probably slightly higher, as some animals were identified only to genus or a higher level.

During the first seven weeks of decomposition, the birch leaves were colonised by a species-rich microarthropod community. There was a certain increase in Collembola species during late autumn and winter (sampling II), but not in Oribatei and Mesostigmata. The highest number of species was noted at the third sampling among Collembola and Oribatei, and in the last sampling among Mesostigmata.

The number of species depends to some degree on the number of litter bags harvested. To correct for that, species numbers in 32 random bags from the last three samplings were compared with that found in the corresponding number of bags at the first sampling. With this correction, the number of Collembola species in the four samplings were 18, 23, 21, 21, and for Oribatei 32, 30, 36, 38. This reinforces the impression of a very rapid establishment of a complex microarthropod fauna. The corrections indicate that the maximum number of Oribatei species is reached at a later stage of decomposition than for Collembola. The adjusted numbers for Collembola species new to the system were 18, 5, 2, 2, and for Oribatei 32, 1, 6, 6.

Even in the diversity index, a difference is noted between Collembola and Oribatei. While the highest value was noted at the third sampling in Collembola, diversity was highest two years later, at the last sampling, among Oribatei. A correction for sample size does not change the picture. Among Mesostigmata, the last sampling gave the highest value, and the third sampling the lowest. Generally, the few identifications to family level or higher were excluded when the diversity index was calculated.

3.1.8. Fauna in a later decomposition stage

The greenhouse experiment mentioned in "Material and methods" was designed mainly to study effects of artificial acidification, and a full faunal survey will be presented later. However, the experiment may also indicate successional changes in a more advanced decomposition phase than achieved in the field experiment. During a dry weight reduction from 63% to 44% of initial weight, no additional microarthropod species colonised the leaves, except for one Collembola species in low numbers. Neither was there any noteworthy loss of species. The most striking change was a general reduction in the microarthropod populations, both among Collembola and all mite groups. For total microarthropoda, the loss was 60%. Because the reduction was most striking among Astigmata (*Schwiebea* cf. *nova* and *S.* cf. *cavernicola*), both Collembola and Oribatei increased their relative importance.

Only a few microarthropod species showed increased mean abundance during this period: *Onychiurus absoloni*, *Neelus minimus* and "other Sminthuridae" among Collembola, *Oppia*

Table 1. Succession and species diversity of Collembola, Oribatei and Mesostigmata in litter bags¹

Sampling	I	II	III	IV
Date (bags laid out 28. 7. 1975)	19. 9. 1975	28. 4. 1976	2.—9. 11. 1976	10. 11. 1978
Collembola				
Number of species in Fig. 1	13	14	15	14
Scarce species (< 1 per bag):				
<i>Isotoma viridis</i> BOURLET	×	×	×	×
<i>Orchesella bifasciata</i> NICOLET	×	×	×	×
<i>Mesaphorura yosii</i> RUSEK	×	×	×	×
<i>Vertagopus</i> sp. (n. sp.?)	×	×	×	—
<i>Entomobrya marginata</i> (TULLBERG)	×	—	—	—
Sminthuridae (mainly juv.)	—	×	×	×
<i>Proisotoma minima</i> (ABSOLON)	—	×	—	×
<i>Pseudanurophorus binoculatus</i> KSENEMAN	—	×	×	—
<i>Isotoma hiemalis</i> SCHÖTT	—	×	—	—
<i>Anurida forsslundi</i> (GISIN)	—	×	—	—
<i>Isotoma violacea</i> TULLBERG	—	—	×	×
<i>Neelus minimus</i> (WILLEM)	—	—	×	×
<i>Folsomia quadrioculata</i> (TULLBERG)	—	—	×	—
<i>Cryptopygus bipunctatus</i> (AXELSON)	—	—	×	—
<i>Anurida pygmaea</i> BÖRNER	—	—	×	—
<i>Isotoma blekeni</i> LEINAAS	—	—	—	×
Number of species	18	23	26	22
Species new to the system	18	6	6	1
Species regained	0	0	0	1
Species lost since last sampling	0	1	3	6
Species permanently lost	0	1	2	6
Shannon-Wiener index H'	1.61	1.71	2.28	1.94
Oribatei				
Number of species in Fig. 2 & 3	23	23	23	23
Scarce species (< 1 per bag):				
<i>Liacarus</i> cf. <i>coracinus</i> (C. L. KOCH)	×	×	×	×
<i>Carabodes femoralis</i> (NICOLET)	×	×	×	×
<i>Carabodes labyrinthicus</i> (MICHAEL)	×	×	×	×
<i>Caleremaeus monolipes</i> (MICHAEL)	×	×	×	×
<i>Scheloribates</i> sp.	×	×	×	×
<i>Pergalumna nervosus</i> (BERLESE)	×	×	×	×
Chamobatidae sp.	×	×	×	—
<i>Autogneta parva</i> FORSSLUND	×	—	×	—
<i>Platynothrus peltifer</i> (C. L. KOCH)	×	—	×	—
<i>Scheloribates laevigatus</i> (C. L. KOCH)	—	×	×	×
<i>Paraleius</i> cf. <i>leontonycha</i> (BERLESE)	—	×	×	—
Palaeacaridae	—	—	×	×
Euphthiracaridae	—	—	×	×
<i>Camisia</i> cf. <i>lapponica</i> TRÄGHÅRDH	—	—	×	×
<i>Camisia spinifer</i> (C. L. KOCH)	—	—	×	×
<i>Belba</i> cf. <i>compta</i> KULCZYNSKI	—	—	×	×
<i>Carabodes marginatus</i> (MICHAEL)	—	—	×	×
<i>Licneremaeus licnophorus</i> (MICHAEL)	—	—	×	×
<i>Zygoribatula</i> cf. <i>trigonella</i>	—	—	×	—
BULANOVA & ZACHVATKINA				
<i>Eupelops geminus</i> (BERLESE)	—	—	×	×
<i>Parachipteria</i> cf. <i>willmanni</i> (V. D. HAMMEN)	—	—	×	×
<i>Belba</i> sp.	—	—	×	—
<i>Ceratozetes</i> sp.	—	—	—	×
<i>Hypochthonius rufulus</i> C. L. KOCH	—	—	—	×
<i>Camisia biurus</i> (C. L. KOCH)	—	—	—	×
<i>Oppia</i> cf. <i>translamellata</i> (WILLMANN)	—	—	—	×
Number of species	32	32	45	43
Species new to the system	32	2	11	4
Species regained	0	0	2	0
Species lost since last sampling	0	2	0	6

Sampling	I	II	III	IV
Date (bags laid out 28. 7. 1975)	19. 9. 1975	28. 4. 1976	2. — 9. 11. 1976	10. 11. 1978
Species permanently lost	0	0	0	6
Shannon-Wiener index H' (adults)	1.23	1.23	1.62	2.61
Mesostigmata				
Number of species in Fig. 3	10	10	9	11
Scarce species (< 1 per bag):				
<i>Pergamasus robustus</i> OUDEMANS	×	×	×	×
<i>Gamasina</i> indet.	×	×	×	×
<i>Pergamasus</i> sp.	×	—	—	—
<i>Veigaia cerva</i> (KRAMER)	—	×	—	×
Number of species	13	13	11	14
Species new to the system	13	2	0	0
Species regained	0	0	1	3
Species lost since last sampling	0	2	3	0
Species permanently lost	0	1	0	0
Shannon-Wiener index H'	1.79	1.89	1.43	2.09

¹) Abundance data for species achieving abundance above one per litter bag have been illustrated in Fig. 4—6. The occurrence of species with lower abundance are indicated by × in the table.

ornata and *Suctobelba* spp. among Oribatei, and Zerconidae among Mesostigmata. Of these, *O. absoloni*, *Suctobelba* spp. and Zerconidae were found to increase gradually during decomposition in the field experiment.

3.2. Horizontal variation in faunal changes

The colonisation pattern and change in fauna during decomposition differed to some extent between replications (blocks) in the field experiment. Such block effects, together with some non-significant tendencies, are presented in Table 2. It is interesting that all the typical "pioneer" species are on the list: *Tyrophagus* cf. *fungivorus*, *Oribatula tibialis*, *Autogneta trögårdhi*, *Entomobrya corticalis* and *Lepidocyrtus cyaneus*. Very high numbers of *T.* cf. *fungivorus* and *L. cyaneus* were developed only in blocks 1—2, while mass occurrence of *E. corticalis* occurred in blocks 3—4. *O. tibialis* achieved highest abundance in block 1, while *A. trögårdhi* was generally more abundant in blocks 1—3 than in block 4.

Chamobates incisus was almost restricted to blocks 2—3, *Oppia ornata* to blocks 3—4, and *Pergamasus* cf. *lapponicus* to block 4.

On the group level, Prostigmata had the highest abundance in block 4 and lowest in block 1 at samplings I, II and IV. The total Oribatei abundance was lowest in bags from block 4 in the three first samplings.

3.3. Comparison with fauna in surrounding soil

In the actual forest site, needles from Norway spruce were the dominant litter component before the clear-cutting. For the soil fauna, birch leaves had been one of the less abundant substrates to live in and feed upon. It is therefore of interest to compare the microarthropod fauna of the birch leaf samples with that of the surrounding soil.

Species lists of Oribatei from the clear-cut area exist from 20 soil samples (each 10 cm²) taken between the experimental plots in the middle of November 1977 (KJØNDAL 1980), and from 480 samples (each 5.3 cm²) taken from different treatments on 16—17 October 1978 (HÅGVAR & AMUNDSEN 1981). The samples, which were evenly distributed on all four replications, included the O-layer (0—3 cm) and the A_c layer (3—6 cm). The 1978 samples were from plots planted with small Norway spruce and Scots pine, but litter fall from these was still insignificant. It turned out that the birch litter bags contained practically all Oribatei species which had been encountered from soil samples on the clear-cut area. Only

Table 2. Horizontal variation (between replications, or blocks) in mean numbers per litter bag of some Microarthropoda¹⁾

Replications (Blocks):		B1	B2	B3	B4	Significance
Astigmata	I	533.5	735.8	13.5	2.3	B3 & B4 < B1 & B2***
<i>Tyrophagus</i>	II	86.8	77.3	19.3	33.3	
<i>cf. fungivorus</i>	III	54.8	29.3	5.5	6.3	
	IV	0.0	0.0	0.0	0.0	
Prostigmata, total	I	68.5	231.3	220.8	736.8	B1 & B2 < B4**
	II	46.8	77.5	211.0	343.8	
	III	35.3	45.3	48.8	20.0	
	IV	140.6	251.9	293.9	464.5	
Oribatei	I	0.0	0.0	9.6	5.4	B1, B2 & B4 < B3** B1 & B2 < B3**, B4 < B3*
<i>Oppia ornata</i>	II	0.0	0.0	9.5	1.0	
	III	0.0	0.0	21.7	6.3	
	IV	0.0	0.9	4.4	1.6	
<i>Autogneta trögårdhi</i>	I	56.6	45.1	55.8	21.4	
	II	33.1	14.1	41.2	5.5	
	III	5.8	2.8	2.8	0.9	
	IV	2.5	0.6	4.4	0.6	
<i>Oribatula tibialis</i>	I	164.3	86.5	60.9	14.8	B3 & B4 < B1**, B2 < B1* B2, B3 & B4 < B1*
	II	208.5	92.7	44.9	28.6	
	III	15.7	4.4	2.9	1.3	
	IV	0.3	0.6	0.3	0.9	
<i>Chamobates incisus</i>	I	0.0	3.3	2.3	0.1	B1 & B4 < B3*
	II	0.0	2.0	4.6	0.6	
	III	0.1	0.4	0.2	0.1	
	IV	0.0	0.1	0.4	0.4	
Oribatei, total ²⁾	I	406.3	178.6	324.6	131.4	B2 & B4 < B1* B4 < B3*, B4 < B1*** B3 < B1*, B2 < B1**
	II	574.4	293.3	362.9	167.1	
	III	144.4	146.6	114.1	76.9	
	IV	103.0	111.6	180.3	121.9	
Mesostigmata	I	0.0	0.0	0.0	0.5	
<i>Pergamasus</i>	II	0.0	0.0	0.0	0.0	
<i>cf. lapponicus</i>	III	0.0	0.0	0.0	3.3	
	IV	0.0	0.0	0.0	9.5	
Collembola	I	3.4	49.4	102.1	101.3	B1 & B3 < B4**
<i>Entomobrya</i>	II	0.2	1.9	0.7	5.1	
<i>corticalis</i>	III	5.3	3.4	5.7	15.1	
	IV	0.0	0.0	0.1	0.5	
<i>Lepidocyrtus</i>	I	85.8	101.0	5.0	9.9	B3 & B4 < B2***, B3 & B4 < B1** B3 & B4 < B2***, B3 & B4 < B1**, B1 < B2* B3 & B4 < B1*, B3 < B2*
<i>cyaneus</i>	II	9.4	14.5	1.4	3.1	
	III	11.9	11.0	2.1	4.1	
	IV	18.1	9.8	12.0	7.6	

¹⁾ I—IV = different samplings. Significance levels: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

²⁾ I: Non-watered and control-watered plots; II—IV: Control-watered plots.

four rare species were not found in the litter bags: *Quadroppia quadricarinata* MICH., *Oppia cf. maritima* (WILLM.), *Oppia cf. translamellata* (WILLM.) of another type than in litter bags, and *Oppia* sp.

Ten of the rare species in the litter bags were not found in the soil samples, although they must have been present in the soil. It should here be noted that not all rare species were identified in the 1978 soil material. Brachychthoniidae were not included in these considerations, except for *Brachychthonius zelawaiensis*.

From the soil samples, it was also clear that practically all Oribatei species could be found in the 0–3 cm layer. This means that the litter bags, which had been inserted into the O-layer, had contact with most, or all, Oribatei species in the soil. Colonisation success would then be purely a question of preference and of life conditions in the new medium.

While qualitative differences in Oribatid fauna were small between soil and litter bags, the quantitative differences were pronounced. The three most abundant species in the early phase of birch leaf decomposition, *Oribatula tibialis*, *Autogneta trögårdhi* and *Eupelops duplex*, all belonged to the rare species in the soil samples. The four most abundant Oribatei in soil during autumn were *Tectocephus velatus*, *Brachychochthonius zelawaiensis*, *Nothrus silvestris* and *Suctobelba* spp. Of these, *N. silvestris* was always rare in the bags (Fig. 3). So was *B. zelawaiensis*, but with increased abundance at the last sampling (Fig. 2). *Suctobelba* spp. increased more markedly in the last sampling (Fig. 2), while *T. velatus* maintained a fairly good abundance from the time of the second sampling (Fig. 3). Although the abundance cannot be compared with that of the "pioneer" species, *T. velatus* was among the more dominant Oribatei species in the litter bags at the two last samplings (Fig. 3).

The relationship between the Collembola fauna in the litter bags and surrounding soil seemed to be parallel to that observed in Oribatei. Comparisons have been made with the Collembola fauna on a corresponding clear-cut area nearby, studied during one year by LEINAAS (1976). All the nineteen most abundant species in his study, with dominance values above 0.1 %, occurred in the birch litter bags. Differences in species composition were due to very rare species, and such differences are to a large degree accidental. However, the abundant "pioneer" species in the bags, *Entomobrya corticalis* and *Lepidocyrtus cyaneus*, were both rare in soil samples. *Friesea mirabilis*, with a very high abundance in the second litter bag sampling (Fig. 1), was among the more abundant soil species. A gradual change towards the typical soil fauna during decomposition of birch leaves is seen by the fact that the four most common Collembola species at the last sampling (*Onychiurus absoloni*, *Isotomiella minor*, *Isotoma notabilis* and *Onychiurus armatus* s.l., Fig. 1), were all were among the nine most common soil species in LEINAAS' (1976) study.

Also among Mesostigmata and Astigmata, a gradual change towards a soil fauna is evident by comparing with the 1978 soil samples (HÄGVAR & AMUNDSEN 1981). *Veigaiia nemo-rensis*, *Pergamasus* cf. *lapponicus*, *Parazercon sarekensis* and *Schwiebia* cf. *nova*, all with highest abundance at the last litter bag sampling, belong to the abundant soil species. On the other hand, the "pioneer" species *Tyrophagus* cf. *fungivorus* was very rare in soil samples.

3.4. Gut contents of selected species

In the study of succession, it is of interest to know the main food items of the fauna in the various stages of litter decay, and also whether the feeding habits of each species may change during decomposition.

The gut contents were studied in selected species of adult Oribatei and adult or nearly adult Collembola, all taken from field litter bags. After the animals were cleared in a boiling drop of Hoyer's medium (under a cover slip), they were crushed to display the gut components. In large Oribatei, the gut boluses sometimes had to be dissected out. Under 600× magnification with interference contrast, the gut contents were classified into fungal spores, fungal hyphae, leaf material, amorphous material without any recognizable structure, and exuviae. The proportion of animals with the different categories of gut contents at various samplings is shown in Fig. 6 for six Collembola species, four Oribatei species and one Astigmata species. Components in brackets indicate only small amounts. The amorphous material was in colour light in the Collembola species and brown in *Eupelops duplex*. Its origin and nature is obscure. In most species, the gut contents were described for 20 to 30 animals or more from each sampling. As the percentage of animals with empty guts varied considerably, often a large number of specimens had to be checked. For instance, in *Entomobrya corticalis* and *Lepidocyrtus cyaneus*, only about 10 %, or even fewer, of the animals had gut contents.

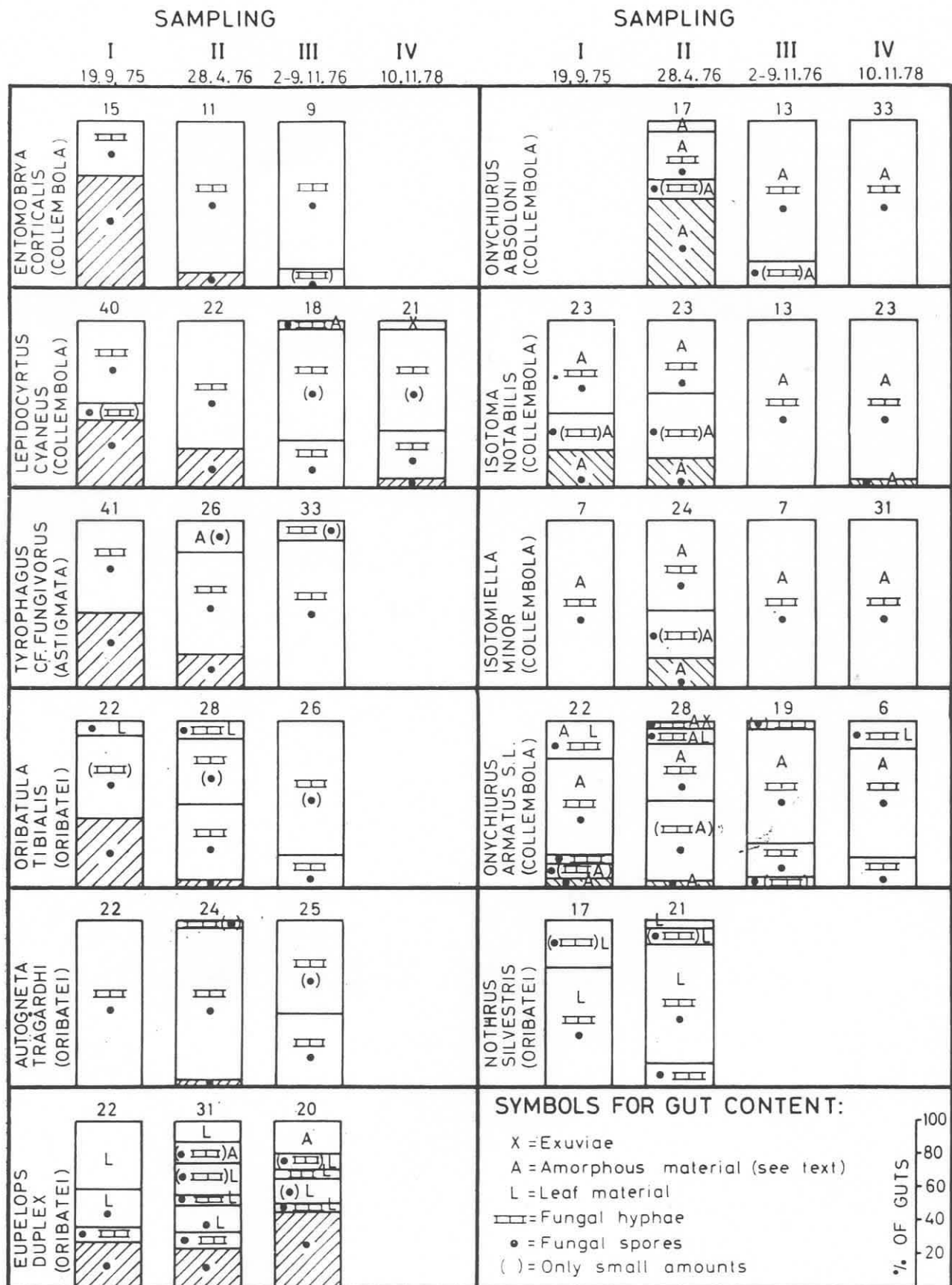


Fig. 6. Gut contents of six "pioneer" species (left column), of four "late" species (upper right) and of *Nothrus silvestris*, a rare species throughout the study. To facilitate the overview, areas indicating guts with only spores, or spores together with amorphous material, have been hatched.

The left half of Fig. 6 contains the "pioneer" species, which totally dominated the microarthropod fauna at the first sampling. Except for the least common of them, *Eupelops duplex*, they were all typical "microphytophagous" species with gut contents consisting of fungal hyphae and spores in all the samplings drawn in the figure [for terminology of feeding habits, see SCHUSTER (1956) and LUXTON (1972)]. However, in the four upper species (*Entomolrya corticalis*, *Lepidocyrtus cyaneus*, *Tyrophagus* cf. *fungivorus* and *Oribatula tibialis*), there was a remarkable change in the relative proportion of spores and hyphae with time. At the first sampling, a considerable proportion of animals from all four species contained exclusively spores in the gut. A smaller percentage of such guts was observed at the second sampling, while none was found in the third. Most guts of *Lepidocyrtus cyaneus* in the two last samplings, and of *Oribatula tibialis* in the third sampling, contained mainly hyphae, with only a small fraction of spores.

Autogneta trögårdhi nearly always contained a mixture of spores and hyphae. However, in the last sampling, the proportion of spores was very low in most guts.

The large species *Eupelops duplex* differed from the other pioneer species in containing leaf material as a component in several guts from all the three first samplings. The species was also special in containing a large number of pure spore-containing guts also at the third sampling.

The right part of Fig. 6 describes gut contents from four species with highest abundance at the last sampling (*Onychiurus absoloni*, *Isotoma notabilis*, *Isotomiella minor* and *Onychiurus armatus* s.l.), and one species with low abundance throughout the study (*Nothrus silvestris*). The four "late" species chosen were also microphytophagous, although some leaf material could be found in *Onychiurus armatus* s.l. In the two last samplings, most animals in all four species contained a mixture of spores, hyphae and amorphous material. Earlier, guts with only spores were recorded among these species also (sampling I and II). A gradual reduction in the importance of spores in gut contents was thus observed in all the typical microphytophagous species studied, regardless of the decomposition phase at which the species were most abundant.

The large *Nothrus silvestris* contained a mixture of spores, hyphae and leaf fragments in most guts from both first and second samplings.

In this context it should be pointed out that the abundance of the typical macrophytophagous (leaf-eating) group, Phthiracaridae, increased in abundance with time (Fig. 3).

4. Discussion

4.1. Introductory remarks

Reservations must be made as to whether the observed faunal changes during decomposition correspond to natural situations. Leaves were laid out earlier than natural leaf fall time. Furthermore, larger invertebrates, e.g. Lumbricidae and predaceous Coleoptera, were excluded from the bags. Lumbricidae were, however, rare in the soil in question. The litter layer in the bag was also abnormally thick (3 cm) and was inserted into the O-layer, being in contact with surrounding organic material at all stages of decomposition. As the leaves were packed vertically, the litter bag content did not shrink notably during the study. Normally, leaves move gradually down the profile as decomposition proceeds. However, since all species in the whole O-layer had continuous access to the leaves, the faunal changes express very well real preferences for different decomposition phases. In natural leaf litter, we do not know to what degree the faunal changes during decomposition are due to the gradual change in vertical position.

As pointed out by USHER & PARR (1977) the term "succession" is used for decomposer communities in two different contexts. One is the change in the decomposer community over long periods of time as the whole ecosystem develops through different seral stages to a potential and rather stable endpoint, usually referred to as a "climax". The other process is exemplified by the present study. It concerns the changes in the decomposer com-

munity during the breakdown of a specific subject, i.e. a leaf, a cone, etc. In this type of succession, the organisms eventually exhaust their own resources and have continuously to colonise new subjects.

4.2. Indications of succession

4.2.1. Population trends

The faunal succession during the decomposition process is due to changes in the substrate, which again influence microhabitat diversity, food availability, etc. Natural population changes in each species during the year due to the life cycle, and any changes within or between years caused by climatic factors, are not successional effects. A major problem in this type of study is to identify and eliminate those factors which tend to obscure the real succession.

In the present case, it is not possible to rule out the modifying effects of climate. We may, however, exclude changes due to life cycles by comparing samples taken at approximately the same time of the year. The samplings I, III and IV were all taken in autumn, but sampling I one and a half months before the other two. In a study of population changes in Collembola performed a few years earlier in the same area (LEINAAS 1976), there were, however, no significant changes during this autumn period in the following species, which are included in Fig. 1: *Friesea mirabilis*, *Onychiurus asotoni*, *Isotoma notabilis*, *Onychiurus armatus* s.l., *Willemia anophthalma* and *Folsomia sensilis*. Neither was the abundance significantly changed at the time corresponding to sampling II (late April). If LEINAAS' (1976) data on these species are representative also for other years, none of the observed changes in the litter bags are likely to be due to their life cycle. Corresponding abundance data on *Isotomiella minor* show that samplings I and II were taken in periods with a somewhat higher abundance than at samplings III and IV. This reinforces the impression of increased abundance of this species during decomposition. According to LEINAAS (pers. comm.), population changes of *Lepidocyrtus cyaneus* are insignificant from late September to early November, which allows comparison of sampling I with III and IV. Sampling II should be disregarded in succession studies, as mortality is large in spring (egg-laying). In *Lepidocyrtus lignorum*, comparisons should be limited to samplings III and IV, as mortality is large during autumn after egg-laying (LEINAAS, pers. comm.).

Relevant data on population changes in the most abundant Oribatei species have not been found. However, the large abundance of adult *Oribatula tibialis*, *Autogneta trågårdhi* and *Eupelops duplex* both in late September (sampling I) and in late April (sampling II) shows that these species overwinter as adults. It is reasonable that population changes during this period are small. In that case, all four samplings can be useful in describing successional trends.

A remarkable increase in *Friesea mirabilis* occurred in the bags between the first and second samplings, i.e. during late autumn and winter. This must be due to pure immigration, as the species reproduces in July and August, i.e. before the first sampling (LEINAAS 1976). The dominance within Collembola was over 50 %, which is larger than in any of the "pioneer" Collembola. In the autumn, *F. mirabilis* was again rare in the bags, although changes in field populations between these points of time should be insignificant (LEINAAS 1976).

We may conclude from this discussion that several of the population changes observed probably reflect true successional changes.

Lack of correction of the observed population data puts in question several published studies about "succession" of invertebrates during decomposition. Especially in successional studies covering only one year, parallel samples from adjacent soil should be taken for comparison. For eurytopic species, for example, the population changes noted after the initial colonisation phase may only be natural seasonal variations. However, some long-term studies strongly indicate successional changes in microarthropod fauna during decomposition of forest litter. We should mention Mesostigmata species in leaves of *Pinus*,

Quercus and *Cornus* (METZ & FARRIER 1969) and Oribatei species in leaves of *Fagus* and *Castanea* (ANDERSON 1975). HUHTA et al. (1979) found marked changes in microarthropods and other invertebrates during three years in a decomposing mixture of sewage sludge and crushed bark.

4.2.2. From litter fauna to deeper-living forms

In addition to confirming population changes in a number of species due to succession processes, we may look for larger-scale patterns. The present data indicate that surface-active or litter-dwelling forms dominate in the early phase, while deeper-living forms gradually become predominant, just as would be the case with natural leaves moving downwards in the profile. Among the "pioneers", *Lepidocyrtus cyaneus* is a well-known litter inhabitant. *Entomobrya corticalis* is common under bark (GISIN 1960) and may have colonised the bags from neighbouring stumps. *Oribatula tibialis* can be found both in litter and the underlying O_f layer (RIHA 1951; VAN DER DRIFT 1951). It is relatively resistant to drought (VAN DER DRIFT 1951) and has, according to TRAVÉ (1961), a great ability to use temporary habitats. The large size of *Eupelops duplex* indicates that it belongs to the litter community. USHER (1975) found *Eupelops* sp. in the litter horizon, at an average depth of 0.8 cm. *Autogneta trögårdhi* was found by FORSSLUND (1947) in the O_f horizon, but its vertical distribution in detail seems to be unknown. For the Astigmata "pioneer" *Tyrophagus* cf. *fungivorus* no information on vertical distribution has been found. However, its scarcity in ordinary soil samples and its rapid colonisation of the bags indicate that it is an active inhabitant of the uppermost strata.

The three most common Collembola species in the "late" phase, (*Onychiurus asoloni*, *Isotomiella minor* and *Isotoma notabilis*) are typical and very common raw humus inhabitants of the actual forest type, and do not belong to the characteristic litter fauna. These species, especially *I. minor*, may also occur in the mineral layer of this soil type (LEINAAS 1976; HÅGVAR unpubl.). Other less dominant species, with highest abundance at the last sampling, are typically deep-living species, occurring both in O_f and O_h layers, as well as in the underlying mineral layer (A_e): *Onychiurus armatus* s.l., *Willemia anophthalma* and *Mesaphorura tenuisensillata*. This is also the case for *Folsomia sensibilis*, which was absent at the first sampling (LEINAAS 1976, HÅGVAR unpubl.). Brachychthoniidae are about equally distributed among raw humus and the mineral layer in the soil in question (HÅGVAR 1978). The small species of *Suctobelba* spp. are probably raw humus inhabitants without any affinity for litter, as their resistance to drought is low (RIHA 1951). *Porobelba spinosa* was found by USHER (1975) to occur at a mean depth of 1.6 cm in the O_f horizon below the litter, in a Scots pine forest. The Phthiracaridae are often considered as litter-dwellers, but preferences for the O_f or O_h layer also occur (LEBRUN 1965; PANDE & BERTHET 1975; USHER 1975). Interpretations in the present study are difficult as long as the actual species have not been identified. *Schwiebea* cf. *nova* can be considered as a typical inhabitant of the O_f layer (HÅGVAR unpubl.).

Friezea mirabilis, staying between the "pioneers" and the "late" colonisers, also has a medium vertical position in the soil, being characteristic for the O_f layer and only very rarely penetrating into the mineral soil (LEINAAS 1976).

The gradual shift among dominant species from litter forms to species characteristic of deeper layers supports the view that many of the observed changes are true successional effects. LEBRUN & MIGNOLET (1975) and MIGNOLET (1975) also found (although in relatively short-term experiments), that changes in the Oribatei community in decomposing deciduous leaves corresponded to vertical zones in the natural oribatid community.

4.2.3. Species numbers and diversity

GOULDEN (1969) proposed a general pattern for changes in species numbers and diversity in the early developmental phases of a biocoenosis. The first phase is characterized by a rapid immigration of species into the newly-established habitat. A maximum diversity pattern is reached at the end of a second phase, during which common species become less

common and rare species less rare. During the third phase, rare species continue to invade the habitat until it is saturated. In each phase, there is a maximum number of species that can invade the habitat.

The present investigation seems to cover at least two of these phases. A characteristic and intense immigration phase was observed. This may have ended even before the first sampling, after seven weeks. A second phase was also evident, in which the "pioneer" species became less abundant (samplings II and III). In Collembola, "pioneer" species disappeared faster, and maximum diversity was also reached earlier (sampling III) than in Oribatei (sampling IV). Increased abundance of rare species among Collembola and Oribatei was not evident until sampling III and, especially, IV. Thus, in the present case, the two processes characteristic of the second phase seem to have been separated in time. At the last sampling, the microarthropod community may have reached the third developmental phase. Only a few new species had entered the system during the two-year period between the two last samplings.

Sooner or later, both abundance and species numbers will be reduced, as the end-point of this type of succession is an exhaustion of the resources and elimination of the fauna. The greenhouse experiment indicated that when the three initial phases are finished and the system is saturated with species, a fourth phase occurs in which abundance is reduced, but without any reduction in species richness. This phase may be explained by a reduction in the volume of the substrate, but without any reduction in the number of niches (microhabitats, food availability, etc.). We may estimate a fifth phase after that, in which both abundance and species numbers are reduced. This will be initiated when the physical and chemical breakdown has reached a point where the number of available niches is reduced.

Among Oribatei in decomposing chestnut and beech leaf litter, ANDERSON (1975) also recognized the three initial phases mentioned. Species numbers and diversity increased during the first year and then remained relatively constant during the following 9 months. No new species entered the leaves after the first 8–9 months. The more rapid colonisation of birch leaves in the present study may be due to three months' earlier deposition in the field. The slower increase in diversity index of Oribatei, and the longer period during which new species colonised, were probably caused by the unusually low decomposition rate of birch leaves in the present site.

4.2.4. Changes in feeding habits

Characteristic changes in feeding habits were observed during succession, both at the community level and for single species. All "pioneer" species among Collembola and Oribatei (except for *Eupelops duplex*) were microphytophages, and at the first sampling a very large proportion of the gut contents was fungal spores. Later, fungal hyphae became the dominant gut content of "pioneer" species. The same change in feeding habits was also noted for several "late" species, which increased their abundance during decomposition. This over-all pattern probably reflects successional changes in the microflora. The observations imply that the species are rather flexible regarding food items, and adjust the food composition according to what is available at various times. The strong selection of fungal spores in certain situations indicates a high nutritional value.

ANDERSON (1975) also noted changes in gut contents of Oribatei species, as well as for enchytraeid worms and chironomid larvae during decomposition of chestnut and beech litter. It is interesting that during the colonisation phase in his study, both enchytraeids, chironomid larvae and Oribatei fed mainly on fungi, and three mycophagous mite genera formed approximately $\frac{3}{4}$ of adult Oribatei in the bags.

In the early decomposition phase, bacteria and fungi profit by large amounts of water-soluble components of high nutritional value (GYLLENBERG & EKLUND 1974). According to OLSEN (pers. comm.), decomposing birch leaves in Norway are colonised by a high number of fungal species during the first autumn, and many of these will produce spores.

ANDERSON (1975) found that Oribatei ingested fungal spores mainly in later stages (in next summer and autumn, and even more than one year after the start of decomposition).

This probably reflects different periods of maximum spore production in birch and chestnut litter.

The beech and chestnut litter was not attacked by soil animals during the first 6 months after fall, due to the toughness of the undecomposed tissues and their high polyphenol and tannin content. After this period, several Oribatei changed feeding habits from fungi to litter. This was especially evident for typical macrophytophages such as *Steganacarus* sp. and *Phthiracarus* sp., which also increased in numbers (ANDERSON 1975). In the birch litter, these two genera were correspondingly among the "late" colonisers.

In addition to this main trend from an almost purely microflora-feeding community to one with more varied feeding patterns, it is also evident that grazing on fungal material was important throughout the study period. For instance, all the four most dominant Collembola species at the last sampling were typical fungal feeders (Fig. 1 and 6). Fungal material was also an important food source for Oribatei at the end of ANDERSON's (1975) study. As many plant nutrients, of which N is often the most limiting, are rapidly immobilized in fungal biomass, decomposition of hyphae and spores through grazing by microarthropods may increase the availability of nutrients to plant roots.

The food of the very abundant Collembolan *Friesea mirabilis* at the second sampling remains obscure. Of 40 animals taken from this sampling, 26 had no visible gut contents. Most of the others contained a very few spores and small amounts of a light, amorphous material. Obviously the species does not belong to the typical microphytophagous group. It is usually supposed to be predaceous, hunting rotifers and other small animals (GISIN 1960). PETERSEN (1971) observed that the species preyed upon eggs of Collembola. Probably there was a maximum of suitable food items in the bags during the first late autumn or winter, after which the species again left the bags.

Very often, animals were seen under the microscope to carry fungal spores or hyphae on their body surface, thus promoting the spread of microflora to all parts of the litter. *Eupelops duplex*, especially, was usually thickly covered dorsally by spores and hyphae.

Fig. 6 clearly shows that the description of the "feeding habits" of a certain species is a complicated task, which must include various successional stages of the substrate. Various substrates probably also offer different food items. In addition, seasonal variations in the gut contents of litter-inhabiting Collembola have been described by ANDERSON & HEALEY (1972).

Due to the many factors regulating food choice in microarthropods, comparisons with literature data are of limited value. It should be mentioned, however, that *Oribatula tibialis* was considered as a fungus- and algae feeder by WALLWORK (1967), and *Nothrus silvestris* is generally considered to be a nonspecialized feeder, ingesting both fungal and leaf material (MURPHY 1956; SCHUSTER 1956; WALLWORK 1967; ANDERSON 1975). The Collembola *Onychiurus armatus* s.l., *O. absoloni*, *Isotoma notabilis* and *Isotomiella minor* have been found to ingest more or less fungal hyphae in other studies as well (POOLE 1959; BÖDVARSSON 1970 and 1973).

A very high number of species coexisting in the bags during the first autumn, before any visible physical breakdown of the leaves occurred, may indicate an excess of microbial food during this phase. Later, when microbial activity decreased and the leaves disintegrated and excrements accumulated, a larger diversity of microhabitats may have become increasingly important to sustain large species numbers.

ANDERSON (1975) assumed that litter-feeding Oribatei might generally have an excess of food, and suggested that spatial, rather than nutritional, properties of the leaf litter determined the number of animals it contained. This view, focusing on available leaf volume as a main factor for animal numbers, is in accordance with a general drop in microarthropod numbers from the "early" to the "late" phase in the greenhouse experiment.

4.2.5. A preference situation

Because the litter bag contents did not change vertical position during the experiment, apart from being slightly covered by birch litter, all microarthropod species in the relevant

O-layer had continuous access to the substratum. Even in this situation, decomposition started with a litter fauna and gradually changed to a soil fauna. The litter species left the leaves after the initial leaching phase, although the bags were still easily available to them. Deeper-living species were not active colonisers at the start, but invaded the leaves mainly after 1–3 years. This indicates that both litter-dwelling and soil-dwelling microarthropods discriminate between substrates of various decomposition phases, and that each group prefers that phase which is normal for their respective vertical layers.

4.3. The colonisation phase and the strategy of “pioneer” species

As decomposition of deciduous leaves is usually a rather fast process, it also represents a rapid case of animal succession. A key factor for an active participation of soil animals in this decomposition is the ability to colonise fresh litter rapidly. In the present case, the highest total abundance of microarthropods was in fact noted after only seven weeks. At this point, the species number of Collembola, Oribatei and Mesostigmata was also close to the maximum observed at any sampling, and represented the majority of all species recorded over a three-year period.

A rapid migration of microarthropods into decomposing deciduous leaves has been found also in other studies (e.g. MIGNOLET & LEBRUN 1975; MIGNOLET 1975; ANDERSON 1975).

At the first sampling, more than half of the microarthropod numbers were made up by only six species: three Oribatei (*Oribatula tibialis*, *Autogneta trögårdhi* and *Eupelops duplex*), two Collembola (*Entomobrya corticalis* and *Lepidocyrtus cyaneus*) and one Astigmata (*Tyrophagus* cf. *fungivorus*). These species have been considered as “pioneer species”. Some properties were characteristic for these species: (a) They were all scarce in ordinary soil samples from the actual site. The fact that they colonised scattered microhabitats so rapidly and numerously implies that they must be very active. (b) All except *E. duplex* were very unevenly distributed on the various replications. A more even distribution was typical for species dominating in later stages of decomposition. (c) All “pioneers” except *E. duplex* were pure microphytophages.

The strategy of the actual “pioneer” species seems to be a high mobility in the litter layer and a well-developed ability to identify and colonise temporary microhabitats with favourable food items, such as fast-growing, spore-producing fungal colonies. All the “pioneer” species ingested spores from several different fungal species, and spores seem to have been generally preferred even in the vicinity of a rich variety of hyphal forms.

As the microbial “flush” period is short and normally limited to a thin top layer, it is natural that microarthropod species which are specialised to this niche are less abundant compared to animals inhabiting the thick underlaying organic layers. The very uneven horizontal distribution characteristic for these species is more difficult to explain. However, it may be that the life conditions differ more between various plots in the thin litter layer than in the thicker, underlying fermentation and humus layers with more stable microclimatic conditions.

Except for the occurrence of juvenile stages among *Tyrophagus* cf. *fungivorus* and *Eupelops duplex*, the present material does not indicate that other early visitors (*Entomobrya corticalis*, *Lepidocyrtus cyaneus*, *Oribatula tibialis*, *Autogneta trögårdhi* and *Friesea mirabilis*) really reproduced within the litter bags. It may be that several of these species just visited the bags as adults or nearly adults to feed, and that they left the bags again before egg-laying.

4.4. Final remarks

The very uneven “macro”-distribution of litter-dwelling “pioneer” species (within distances of 20–50 m) implies that the succession pattern in the early decomposition phase may vary widely, even within an apparently homogeneous biotope. The microarthropod community in later stages is, however, less variable, and therefore more predictable.

It is a remarkable feature both among Oribatei and Collembola, that practically all species occurring in the surrounding soil colonised the bags, even though birch litter is not

typical for the site. This reflects a high degree of mobility in the whole microarthropod community, and a high tolerance for various substrates.

The three most abundant Oribatei species in the relevant soil, *Tectocepheus velatus*, *Brachychochthonius zelawaiensis* and *Nothrus silvestris*, were never really abundant in the bags. This may be due to the high pH level in the leaves (above 5). All species are strongly reduced in the field if soil pH is raised above 4.5 by liming (HÅGVAR & AMUNDSEN 1981).

The present experiment illustrates the value of rare species in a system. When special conditions are created locally (or if the whole system is influenced by unpredictable factors), rare species may be the most suited to the new conditions and temporarily or permanently take over important functions. ABRAHAMSEN & THOMPSON (1979) demonstrated this very clearly for Enchytraeidae in an urea fertilization experiment in a poor coniferous forest. An extremely rare species in this habitat, *Enchytraeus buchholzi* VEJDOVSKY, which is typical for very rich soils, showed a large peak in abundance two years after fertilization. Later, when the soil conditions returned to a normal state, the species again became very rare.

The relatively dry summer in 1976 may be a reason for the general low abundance of microarthropods in sampling III. Another reason may be that the "pioneer" species had largely withdrawn from the bags, while the typical soil-living species had not yet reached high numbers. This occurred the next year (sampling IV).

4.5. Suggestions for further studies

Some suggestions for future successional studies may be made on the basis of the present work. First, one should try to design experiments so that natural conditions are achieved as nearly as possible. Modifying effects of climate and natural population changes may be identified and eliminated by taking parallel samples from the surrounding soil. The colonisation phase should be followed by frequent sampling (weekly or monthly). It is important to include even the last phases of decomposition. We know very little about how diversity changes, and the pattern by which species numbers and abundance are reduced when the resources are gradually exhausted. The present study also indicates that substantial faunal changes may occur during winter. To understand the dynamics and the successional changes in the community, studies of gut contents, age distribution and vertical occurrence of dominant species are rewarding. If possible, a simultaneous study of microfloral succession should be carried out. Changes in leaf chemistry, especially the content of polyphenols and tannins, ought to be followed. Eventually, further clarification of the limiting factors for species numbers and total animal abundance in various phases is a challenge which may result in important ecological information.

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6. Summary . Résumé

Succession of microarthropods in decomposing birch leaves [mixture of *Betula pubescens* EHRL. and *B. verrucosa* EHRL.] was studied during a three-year period. The leaves were kept in litter bags under small *B. verrucosa* plants (0.5–1 m) on a clear-cut area with a podzol soil (Typic Udipsamment) in a Norway spruce/Scots pine forest. Litter bags were laid out 28. 7. 1975 and sampled on 19. 9. 1975, 28. 4. 1976, 2.–9. 11. 1976 and 10. 11. 1978. An intense immigration phase was observed. At the first sampling, the majority of all species recorded from bags over three years were already present, and the abundance was the highest in the study. However, more than half of the numbers were made up by only six "pioneer" species, belonging mainly to the litter fauna: three Oribatei [*Oribatula tibialis* (NICOLET), *Autogneta trögårdhi* FORSSLUND and *Eupelops duplex* (BERLESE)], two Collembola [*Entomobrya corticalis* (NICOLET) and *Lepidocyrtus cyaneus* TULLBERG], and one Astigmata [*Tyrophagus* cf. *fungivorus* (OUDEMANS)]. A second phase was observed during the later samplings, in which diversity increased and species characteristic for deeper layers took over the dominance. It was shown for several species that the changes in abundance and dominance were not due to their life cycle patterns, but probably reflected true successional changes. A third phase, in

which the last rare species were invading the substrate, was believed to occur at the end of the study period. A laboratory experiment indicated that when the habitat was saturated with species, a fourth phase occurred, in which the abundance was reduced in most species, but practically without changes in species composition. A fifth phase is predictable, in which both abundance and species numbers are reduced, as the resources are exhausted. Analysis of gut contents showed that all "pioneers" except *E. duplex* were typical microphytophages. All microphytophages studied ingested large amounts of fungal spores in the early decomposition phase, while fungal hyphae later became increasingly important. Practically all Collembola and Oribatei species in the surrounding soil invaded the birch litter, even though the litter type was atypical for the site. However, the relative dominance was different.

Succession, diversité et régimes alimentaires de microarthropodes dans la litière de bouleau en décomposition

La succession de microarthropodes dans la litière de bouleau en décomposition (mélange de *Betula pubescens* EHRL. et de *B. verrucosa* EHRL.) a été étudiée durant trois ans. Les feuilles ont été placées dans des sacs de nylon sous de petits plants de *B. verrucosa* (0,5–1 m) sur une surface déboisée sur sol podzolisé (Typic Udipsamment) dans une forêt de sapins norvégiens/pin d'Ecosse. Les sacs de nylon ont été placés le 28/7/1975 et des échantillons ont été prélevés le 19/9/1975, le 28/4/1976, le 2–9/11/1976, et le 10/11/1978. On a pu observer une phase d'immigration intensive. La majorité de toutes les espèces répertoriées dans les sacs pendant trois ans était déjà présente au premier prélèvement et l'abondance était la plus élevée à ce moment. Pourtant plus de la moitié des effectifs se composaient de six espèces pionnières seulement appartenant principalement à la faune de la litière: trois Oribatei [*Oribatula tibialis* (NICOLET), *Autogneta trågårdhi* FORSSLUND et *Eupelops duplex* (BERLESE)], deux Collemboles [*Entomobrya corticalis* (NICOLET) et *Lepidocyrtus cyaneus* TULLBERG] et un Astigmaté [*Tyrophagus* cf. *fungivorus* (OUDEMANS)]. Une deuxième phase a été observée à l'occasion des échantillonnages récents, durant laquelle la diversité a augmenté et des espèces caractéristiques des couches plus profondes dominaient progressivement. Pour plusieurs espèces il est apparu que les changements d'abondance et de dominance ne sont pas dus aux caractéristiques de leur cycle de vie mais reflètent probablement une véritable succession. On suppose qu'une troisième phase surviendra à la fin de l'étude, durant laquelle les dernières espèces rares envahiront le substrat. Une expérience de laboratoire a montré qu'une quatrième phase pourrait survenir quand l'habitat serait saturé en espèces. Au cours de cette phase l'abondance serait diminuée pour la plupart des espèces et, cependant, sans changement qualitatif du spectre spécifique. Une cinquième phase est prévisible durant laquelle aussi bien l'abondance que le nombre d'espèces seront réduits suite à l'épuisement des ressources. Les analyses du contenu des tubes digestifs ont montré que toutes les espèces pionnières à l'exception de *E. duplex* sont des microphytophages typiques. Tous les microphytophages étudiés ont ingéré de grandes quantités de spores de champignons à une phase peu avancée de la décomposition tandis que plus tard les hyphes des champignons sont devenus plus importants dans leur alimentation. Pratiquement toutes les espèces de Collemboles et d'Oribates du sol contigu ont envahi la litière de bouleau contenue dans les sacs même si la litière est étrangère au site étudié. Cependant, le spectre d'abondance relative est différent.

Mots clé: Succession, diversité, contenu de tube digestif, microarthropodes, décomposition, litière de bouleau.

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